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Evolution of Gamete Motility Differences I. Relation Between Swimming Speed and Pheromonal Attraction

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An analysis is made using population genetic models of the evolution of gamete motility differences as a consequence of a pheromonal gametic approach mechanism. A stable swimming speed dimorphism may arise via disruptive selection on swimming speed, resulting from selection favouring a high efficiency of finding another gamete as well as a high probability of being found by another gamete. It is shown that no more than two different swimming speeds can coexist in a stable polymorphism. A specific relation is deduced between gamete swimming speed and the surface area of the volume around the gamete bounded by the critical pheromone concentration. It is concluded that an initial difference in swimming speed of at least twofold will lead to a stable dimorphism, and that evolution towards one of the gamete types becoming non-motile is very likely.

1. Introduction

In recent years a number of theoretical studies has been published of various aspects of the evolution of gamete dimorphism. Parker, Baker & Smith (1972) proposed a model for the evolution of anisogamy based on selection favouring the production of large numbers of gametes as well as a large zygote size. Their ideas were incorporated into a population genetic model permitting a more rigorous analysis by Charlesworth (1978), who confirmed their results. On the same subject, but using a different approach, are contributions by Bell (1978) and Maynard Smith (1978). Hoekstra (1980) has shown in an extension of Charlesworth's (1978) model, that there

cannot be stable anisogamy with more than two different gamete sizes. Models for the evolution of disassortative gamete fusion are studied by Parker (1978), who considers the evolution of disassortative fusion with respect to gamete size in an originally random mating anisogamous population, and by Charlesworth (1978), who shows that disassortative fusion can evolve by selection for close linkage between the loci determining mating types and gamete size. Particularly intriguing is the problem of the evolution of two mating types from an original situation in which all (iso-) gametes are alike functionally. This problem has been analyzed by Hoekstra (1982), who shows that it is difficult to explain. Evolution towards unipolarity in gamete recognition or adhesion (implying the existence of two mating types) requires a more than twofold disadvantage for bipolarity. However, the evolution of mating types is much more likely when a pheromonal attraction mechanism is already present, but such pheromonal systems seem to be rare among isogamous algae.

In this and the following paper another (and hitherto neglected) aspect of gamete dimorphism will be studied: the evolution of motility differences in the presence of a pheromonal attraction system. This paper in particular analyses the relation between swimming speed of gametes and their abilities to find, and to be found by, other gametes.

2. Basic Assumptions

The following assumptions underlie the models of this and the following paper.

(i) A large population of vegetative haploid individuals is living in water. Reproduction may be asexual, but under suitable conditions gametes are formed which fuse at random to form zygotes; these zygotes divide meiotically to form new vegetative individuals. (Many Algae have such a life cycle.)

(ii) There is a pheromonal gamete attraction mechanism. In some of the models all gametes both produce pheromone and respond to it, while in other models there is already a dimorphism in this respect: part of the gamete population only produces pheromone, while the rest only responds (for a model of the evolution of this dimorphism, see section 4 of Hoekstra, 1982). The pheromone diffuses into the water. There exists a critical pheromone concentration, which is the lowest concentration still perceptible by the gametes. The set of all points of this critical concentration forms a closed convex surface in three-dimensional space. The volume bounded by this attraction surface is called the *attraction space*.

(iii) The swimming paths of the gametes are straight lines in random directions. When a gamete moves into the attraction space of another

gamete, it will change direction so as to achieve gamete contact. A gamete's probability of *finding* another gamete in a given time interval is proportional to its swimming speed. A gamete's probability of *being found* by another gamete in a given time interval is proportional to the area of its attraction surface. For a justification of the latter assumption, see Kendall & Moran (1963, chapter 3).

(iv) All genetic variants to be considered in the models have the same fitness with respect to asexual reproduction.

3. Preliminary Population Genetic Analysis

Consider a population in which all gametes produce pheromone and are also able to respond to it. There is a locus A affecting gamete swimming speed with alleles A_1, A_2, \dots, A_k . It is assumed that A_i gametes have swimming speed v_i and attraction surface area s_i . We shall denote the zygote resulting from an A_i gamete finding an A_j gamete as A_iA_j . Let x_i be the frequency of A_i individuals in a given generation. Among the gametes produced, A_i will also have frequency x_i . From the assumptions mentioned in section 2 (iii) it follows that among the zygotes formed, the frequency of A_iA_j is:

$$v_i s_j x_i x_j \sum_{i=1}^k \sum_{j=1}^k v_i s_j x_i x_j. \quad (1)$$

The frequency of A_i among the individuals of the next generation is thus:

$$x'_i = x_i \sum_j \left(\frac{v_i s_j + v_j s_i}{2} \right) x_j / \sum_{ij} \left(\frac{v_i s_j + v_j s_i}{2} \right) x_i x_j. \quad (2)$$

If we write

$$w_{ij} = \frac{v_i s_j + v_j s_i}{2} \quad (3)$$

and

$$\bar{W} = \sum_{ij} w_{ij} x_i x_j \quad (4)$$

equations (2) become:

$$\bar{W} x'_i = x_i \sum_j w_{ij} x_j. \quad (5)$$

Therefore our model is equivalent to a model of a random mating diploid population with genotype A_iA_j having fitness w_{ij} . The properties of the

latter model are off course well-known; if there are just two alleles, A_1 and A_2 , a stable polymorphism will be maintained if

$$w_{12} = w_{21} > w_{11}, w_{22}, \quad (6)$$

and the equilibrium frequencies are given by:

$$\frac{\hat{x}_1}{\hat{x}_2} = \frac{w_{12} - w_{22}}{w_{12} - w_{11}}. \quad (7)$$

Writing $V = v_1/v_2$ and $S = s_1/s_2$, and assuming that A_1 specifies the faster gametes so that $V > 1$, we obtain the following conditions for a stable polymorphism with respect to gamete swimming speed from conditions (6):

$$V + S > 2VS \quad (8a)$$

$$V + S > 2. \quad (8b)$$

Expressed in V and S the equilibrium frequencies (7) become:

$$\frac{\hat{x}_1}{\hat{x}_2} = \frac{V + S - 2}{V + S - 2VS}. \quad (9)$$

Figure 1 shows a graphical representation of conditions (8). A necessary (but not sufficient) condition for polymorphism is that the slower gamete must have a larger attraction surface area. Furthermore it can be seen from

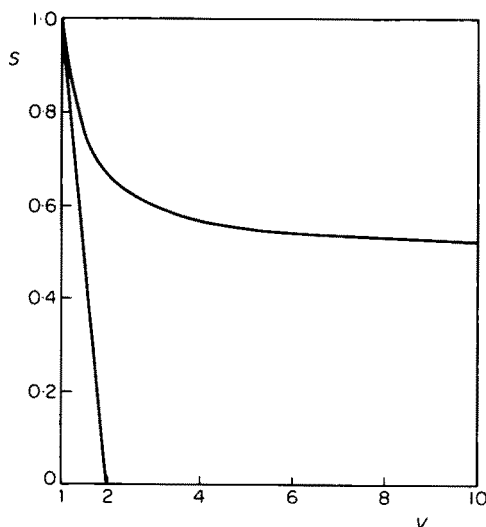


FIG. 1. Graphical representation of conditions (8a) (upper curve) and (8b) (lower curve). There is a stable gamete motility dimorphism for (V, S) values between the two curves.

Fig. 1 that the conditions for gamete motility dimorphism are very restricted when the difference in swimming speed is small ($V \approx 1$), but that they are easier to satisfy for larger values of V . Clearly, we need to know more about the actual relation between swimming speed and attraction surface area, in order to be able to judge the likelihood of such a swimming speed polymorphism. However, before investigating this relation in section 5 of this paper, we ask under what conditions a third swimming speed can be established in a population dimorphic for gamete swimming speed. This question is similar to the question whether there can be more than two gamete sizes, analysed by Hoekstra (1980).

4. Introduction of a Third Swimming Speed

Consider a large population polymorphic for A_1 and A_2 . The inequalities (8) are supposed to be satisfied. A third allele A_3 , specifying an intermediate gamete swimming speed, is introduced into this population. We therefore have $v_1 > v_3 > v_2$ and $s_1 < s_3 < s_2$.

We now examine under what conditions A_3 will be protected (increase in frequency when rare) by linearizing equation (5) in the neighbourhood of $x_3 = 0$. This results in:

$$x'_3 \approx x_3 \frac{w_{13}\hat{x}_1 + w_{23}\hat{x}_2}{w_{11}\hat{x}_1^2 + 2w_{12}\hat{x}_1\hat{x}_2 + w_{22}\hat{x}_2^2} \quad (10)$$

where \hat{x}_1 and \hat{x}_2 are given by equation (7).

Therefore, A_3 is protected if

$$w_{13}\hat{x}_1 + w_{23}\hat{x}_2 > w_{11}\hat{x}_1^2 + 2w_{12}\hat{x}_1\hat{x}_2 + w_{22}\hat{x}_2^2. \quad (11)$$

Writing $V^* = v_3/v_2$ and $S^* = s_3/s_2$ and using equation (3), the inequality (11) can be written in the following form:

$$(VS^* + SV^*)\hat{x}_1 + (V^* + S^*)\hat{x}_2 > 2(V\hat{x}_1 + \hat{x}_2)(S\hat{x}_1 + \hat{x}_2). \quad (12)$$

From equation (9) one obtains

$$\hat{x}_1 = \frac{V+S-2}{2(V+S-1-VS)} \quad \text{and} \quad \hat{x}_2 = \frac{V+S-2VS}{2(V+S-1-VS)};$$

substituting these expressions for \hat{x}_1 and \hat{x}_2 into inequality (12) we obtain after rearranging and simplifying

$$\frac{V-1}{V^*-1} < \frac{1-S}{1-S^*}, \quad (13)$$

or

$$\frac{v_3 - v_2}{v_1 - v_2} > \frac{s_2 - s_3}{s_2 - s_1}. \quad (14)$$

Condition (14) is depicted in Fig. 2. It is not difficult to prove that for condition (14) to be satisfied, the point α_3 must be above the line $\alpha_1\alpha_2$, and that condition (14) cannot be satisfied (and therefore A_3 is not protected) if α_3 lies beneath the line $\alpha_1\alpha_2$. Thus protection of A_3 depends on the relation between gamete swimming speed v and attraction surface area s . If this relation takes the form of an (upward) concave curve on the relevant interval in the s, v plane (the dotted line in Fig. 2), then A_3 will not be protected; and if the relation between s and v is represented by an (upward) convex curve (broken line in Fig. 2), A_3 will invade an A_1, A_2 population.

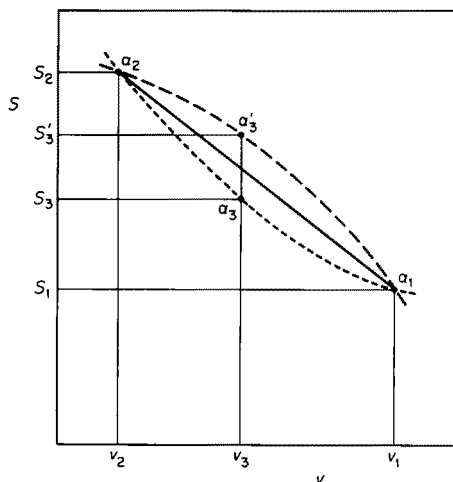


FIG. 2. Graphical representation of condition (14). A (third) intermediate gamete swimming speed will increase in frequency when rare if the relationship between s and v takes the form of an upward convex curve (---), but will be selected against in case of an upward concave relation (.....).

5. Relation Between Gamete Swimming Speed and Attraction Surface Area

Roberts (1923) has studied the density distribution of smoke in a smoke-cloud produced continuously and uniformly at a fixed point in a uniform wind. The diffusion of smoke in the atmosphere from a fixed source in a uniform wind can be considered to be analogous to the diffusion of pheromone in water from a source, moving with constant speed along a

straight line in still water. For this reason we can use a result of Roberts (1923) as a starting point for our analysis. Roberts' approach has also been used by Bossert & Wilson (1963) in their analysis of pheromonal communication by insects.

Let χ be the concentration of pheromone in g/cm^3 ; q the rate of pheromone production in g/sec ; K the diffusion coefficient in cm^2/sec ; r the distance from the source of pheromone production in cm ; v the gamete swimming velocity in cm/sec . Then the pheromone concentration is (Roberts, 1923):

$$\chi = \frac{c}{r} e^{-(vr/2K)(1-\cos\theta)}, \quad (15)$$

where $c = q/4\pi K$.

Note that equation (15) is given in polar coordinates (see Fig. 3). Our objective is to determine the area of the surface of revolution obtained by rotating the upper half of the curve given by equation (15) around the horizontal axis. That area is identical to the attraction surface area defined in section 2 if χ is equal to the critical pheromone concentration. We then want to calculate the relation between this area and the swimming velocity v .

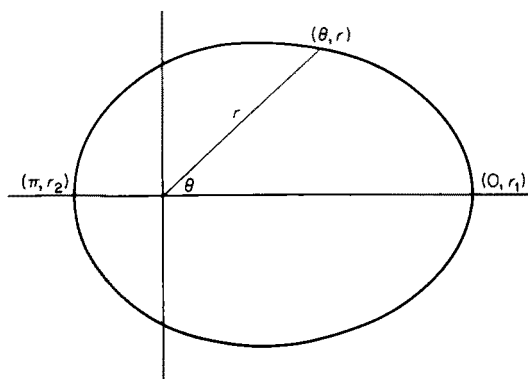


FIG. 3. The curve consists of points of equal pheromone concentration in a plane through a pheromone producing gamete, represented by the origin of the coordinates. The gamete is moving with a constant speed in the negative direction along the horizontal axis.

In general, the area of a surface of revolution obtained by rotating around the x -axis the graph of a function $f(x)$, is equal to

$$2\pi \int_a^b f(x) \sqrt{1 + \{f'(x)\}^2} dx \quad (16)$$

This formula gives the area of the curved surface between the planes $x = a$ and $x = b$. Therefore, we need to know the interval over which the graph given by equation (15) has to be integrated, and also the first derivative of this function.

First, we observe (see Fig. 3) that at the point $(0, r_1)$ equation (15) becomes

$$\chi = \frac{c}{r_1} \quad (17)$$

This means that the length r_1 of the "tail" of the attraction space is determined by the pheromone production and the critical pheromone concentration. Note that the length of the tail does not depend on the swimming speed v . In fact r_1 is equal to the radius of the spherical attraction space of a non-motile gamete (see also Fig. 5). Assume that at a given rate of pheromone production, the critical (i.e. just perceptible) pheromone concentration is equal to χ^* , and the length of the tail r_1 equal to r^* . It is convenient to re-scale our description by expressing the distances involved as fractions of r^* . Let the new variable be $\rho = r/r^*$, ($0 < \rho \leq 1$). Substituting ρr^* for r into equation (15), we obtain for the concentration at point (π, r_2) :

$$\chi = \frac{c}{\rho_2 r^*} e^{-v \rho_2 r^* / K} \quad (18)$$

Equating equations (17) and (18) yields for $\chi = \chi^*$

$$\rho_2 = e^{-v \rho_2 r^* / K} \quad (19)$$

It is not possible to obtain an explicit expression for ρ_2 , but using numerical methods ρ_2 can be computed for varying values of vr^*/K , and then the required integration interval is known. In order to apply formula (16) we have to express equation (15) in rectangular coordinates. Substitution of $r = \sqrt{x^2 + y^2}$ and $\cos \theta = x/\sqrt{x^2 + y^2}$ and rescaling as before by writing $x = \xi r^*$ and $y = \eta r^*$ results in

$$\chi = \frac{c}{r^* \sqrt{\xi^2 + \eta^2}} e^{-(vr^*/2K)(\sqrt{\xi^2 + \eta^2} - \xi)} \quad (20)$$

For the critical concentration $\chi^* = c/r^*$, equation (20) can be written in the following form

$$\eta = \pm \{e^{-(vr^*/K)(\sqrt{\xi^2 + \eta^2} - \xi)} - \xi^2\}^{1/2} \quad (21)$$

With the use of numerical methods the values of η were computed.

Finally, an expression for the first derivative $d\eta/d\xi$ can be derived; this rather lengthy and uninformative expression will not be reproduced here.

Now all the ingredients necessary for obtaining the integral (16) can be computed; the integral itself was approximated numerically using the method of Patterson. In this way the size of the attraction surface area has been computed for a large number of values of v/K ranging from 0 to 25 000. For convenience r^* has been set equal to 1. Realistic values of vr^*/K are of the order of $10^3 r^*$, since gamete swimming speed v in microorganisms is of the order of 10^{-2} cm/sec (Nultsch, 1974), and the diffusion coefficient K in water is of the order of 10^{-5} cm²/sec.

The relation between the attraction surface area s and the swimming speed v appears to be (upward) concave over the whole interval for which the computations have been performed. Figure 4 shows this relation for the

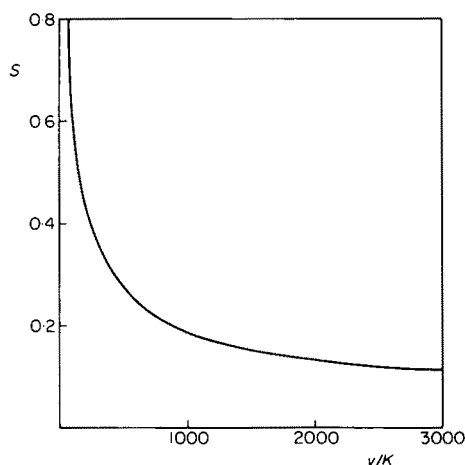


FIG. 4. Relation between s and v/K obtained by computations described in the text.

part of the interval containing the most realistic values of v/K . From this result, in conjunction with the analysis in section 4, we may conclude that a third (intermediate) swimming speed cannot invade a population polymorphic for two swimming velocities. Moreover, if a mutant swimming speed is larger or smaller than the speed of the two established types, the then intermediate type will be unprotected. There is thus disruptive selection in this model for an increasing difference in swimming velocities, perhaps up to the point where one of the two types will abandon the habit of swimming. An analysis of the latter situation will be given in section 6.

Figure 5 shows sections by a plane through the pheromone source (the gamete) of the attraction surface for various swimming velocities.

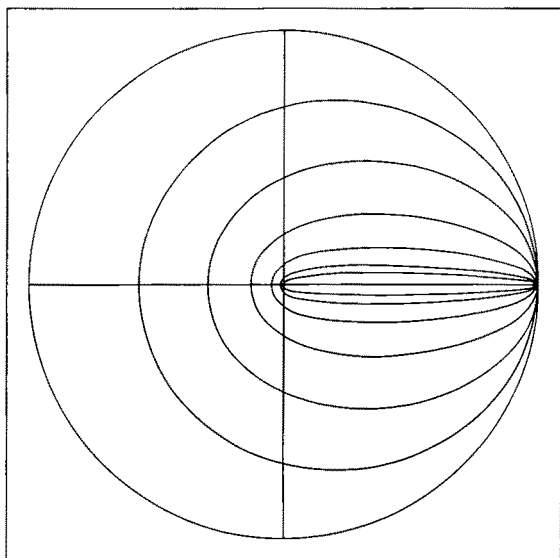


FIG. 5. Contours of the attraction space in a section through the gamete for various swimming velocities. The gamete is at the origin of the coordinates, and is moving with constant speed along the horizontal axis in negative direction. The outer contour is from a non-motile gamete ($v/K = 0$); inwards are contours for successively $v/K = 1, 4, 16, 64, 256$, and 1024.

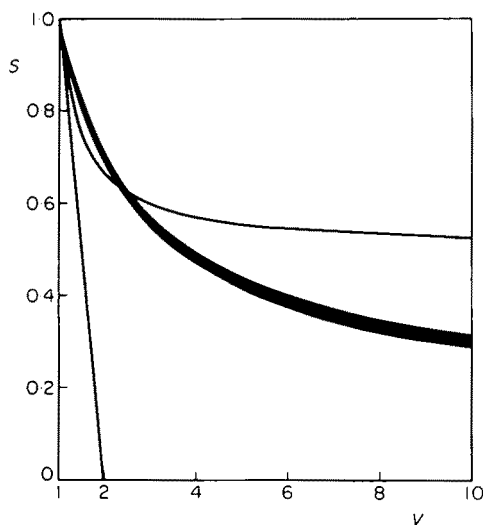


FIG. 6. The computed relation between S and V ; the curves representing this relationship for values of v/K in the interval $(10, 10^4)$ all lie within the black region. A gamete motility dimorphism is possible for S values between the two curves.

In Fig. 6 the results of the computations are given in a form which permits a direct comparison with the conditions for stable polymorphism shown in Fig. 1.

The relation between the ratio S of the attraction surface areas and the ratio V of the swimming velocities of the two types present in a population appears to be nearly independent of the value of v/K for $v/K > 10$. The curves representing the relationship between S and V for all values of v/K in the interval $[10, 10^4]$ are covered by the thick line in Fig. 6. Since most realistic values of v/K are of the order of 10^3 , we may conclude from Fig. 6 that there can be stable polymorphism for gamete swimming speed if the velocities of the two types differ by a factor of at least 2.5.

6. The Special Case of One of the Gamete Types being Non-motile

In so called oogamous species the female gametes are much bigger than the male gametes and non-motile. In some isogamous species (e.g. the brown alga *Ectocarpus*) the female gametes attach themselves to the substrate and remain sessile.

It is therefore of interest to consider the evolution of a non-motile type. In particular we ask under what conditions a non-motile mutant will be established in a population consisting of motile gametes. Substituting $v_2 = 0$ into equation (3) and using inequality (6) provides the following condition for a stable polymorphism of a motile and a non-motile type:

$$s_1 < \frac{1}{2}s_2. \quad (22)$$

Since s_2 is equal to the surface area $4\pi r^{*2}$ of a sphere (with radius r^*), and the ratio s_1/s_2 is independent of r^* , we write condition (22) as

$$s_1 < 2\pi \approx 6.2832. \quad (23)$$

From the computed results described in the preceding section it follows that inequality (23) is satisfied if

$$vr^*/K > 1.33. \quad (24)$$

As mentioned before, reasonable values of v/K are of the order of 10^3 , implying stable polymorphism if $r^* > 1.33 \times 10^{-3}$ cm. This condition seems very easily satisfied, since gamete sizes are also of the order of 10^{-3} cm, and gametes show a characteristic ability to react to very small concentrations of pheromone. If the non-motile gamete is fixed to a substrate, the attraction space will more nearly be represented by a half sphere, the substrate acting as a reflecting plane. Doubling the amount of pheromone produced (i.e. doubling the value of c (see equation (15))), and assuming

the same critical concentration χ^* , we obtain from equation (17) that the radius of this half sphere is twice the original radius r^* . Therefore, the attraction surface area in this case is equal to $\frac{1}{2} \times 4\pi(2r^*)^2 = 8\pi r^{*2}$, which means that the attraction surface area of a gamete fixed to a substrate is twice as large as that of a free floating non-motile gamete. However, the accessibility of the former will be reduced, so that after all the chances of being found are presumably not very different for the two types of non-motile gametes.

7. Discussion

In this study an analysis has been made of the evolution of gamete motility differences as a consequence of a pheromonal gametic approach mechanism. In particular a specific relation has been deduced between swimming speed and attraction surface area, based on a number of assumptions, listed in section 2 of this paper. Two of these assumptions require some additional discussion. First, one might well ask how realistic the assumption of a closed convex attraction surface is in connection with currents and turbulence in the water. However, algal gametes swimming in water are characterized by a Reynolds number (the ratio of the inertial forces to the viscous forces) smaller than one, which implies that the viscous forces of the surrounding water dominate the inertial forces of the moving gamete (Purcell, 1977). Therefore, these gametes cannot "experience" any turbulence in the water. Hence we are justified in setting up the models as if the gametes were in stagnant water (provided the dimensions of the attraction space are small relative to the scale on which turbulence occurs). Second, the assumption that the swimming paths of the gametes are straight lines in random directions, although adequate for some species (like *Ectocarpus*, Müller, 1976), seems unrealistic for other species of micro-organisms. For example, the motility pattern of gametes of the aquatic fungus *Allomyces* is characterized by short, smooth swimming paths more or less along a straight line, interrupted by so-called "jerks" changing the orientation of the gametes (Pommerville, 1978). This pattern is similar to bacterial motility, characterized by "twiddling" and tumbling (Berg & Brown, 1972). The question is whether we are still justified in such cases to assume that for any gamete the probability of detection by another gamete is proportional to its attraction surface area. This assumption was based on a theorem which states that the probability of a random line intersecting a three-dimensional convex region is proportional to the surface area of the region (Kendall & Moran, 1962). It seems safe however to conjecture that the theorem also holds for the swimming patterns just discussed provided all directions are equally likely at any moment.

The results described in section 5 in conjunction with the population genetic analysis of sections 3 and 4 indicate that a mutation with sufficiently large effect on swimming speed will be selected, leading to a stable polymorphism for gamete motility. Furthermore, since an intermediate swimming speed is unprotected, there will be disruptive selection resulting in an increasing difference in swimming speed of the two types. A number of predictions follow from the theory developed in this paper. Firstly, one would not expect to find cases of gamete motility dimorphism with only a small difference in swimming speed between the two types (less than two-fold, say). Secondly, in any population there will be no more than two different types of gametes with respect to swimming speed. Thirdly, species with a chemotactic gamete approach mechanism but without a gamete motility dimorphism would not be expected to exist. Fourth, from equation (9) and the results shown in Fig. 6 it follows that one would expect to find an excess of the faster swimming variants, \hat{x}_1 being considerably greater than \hat{x}_2 even in the case of a tenfold difference in swimming speed. Application of equation (7) in the case of one of the two gamete types being non-motile (section 6) gives $\hat{x}_1/\hat{x}_2 = s_2/(s_2 - 2s_1)$, implying that one would expect more motile than non-motile gametes.

To what extent are these predictions in accordance with the facts? With respect to the first prediction, those species where the slowest (female) gamete settles at a substrate or does not swim are in agreement with the theory; this applies to all oogamous species and to many anisogamous species. Unfortunately we have been able to find only a few reports on actual swimming speeds of gametes. In the fungus *Allomyces marcrogynus* the male gametes swim about 1.6 times faster than the female gametes (Pommerville, 1978), which is in conflict with the prediction. However the female gametes have a tendency to stop swimming after some time, so that after all the prediction does not seem to be violated.

In the subsequent paper (Hoekstra, 1984) a more general population genetic model will be analysed, permitting under certain conditions a stable polymorphism with a smaller difference between the two motility variants.

As far as we are aware, there is no observation contradicting the second prediction. There is however one report in conflict with the third prediction. Tsubo (1961) found that in the isogamous species *Chlamydomonas moewusii* var. *rotunda*, the mating type (−) gametes produce a pheromone which attracts mating type (+) gametes. The only difference in behaviour between the two types of isogametes seems to be that the (−) mating type gametes become non-motile shortly after the initial stages of pair formation, which—in the light of the theory presented in this paper—they were expected to do in an earlier stage. It would be very interesting to confirm Tsubo's results

and to investigate the system further, which is also advocated by Kochert (1978).

As to the fourth prediction, we have not found relevant data to test it. However, the more elaborate models of the subsequent paper (Hoekstra, 1984) predict a 1:1 "sex" ratio. For reasons to be explained in that paper, the latter prediction is based on more realistic assumptions.

Finally, in the light of the theory presented in this paper, it is interesting that (with the exception of the above-mentioned *Chlamydomonas* species investigated by Tsubo (1961)) no isogamous species with sexual pheromones are known. It seems likely that once a chemotactic gamete attraction mechanism has been evolved, isogamous species will either develop a gamete motility dimorphism, thus becoming behaviourally anisogamous like *Ectocarpus*, or evolve towards morphological anisogamy. The latter possibility is analysed in the subsequent paper (Hoekstra, 1984).

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